Effects of simulated drought and nitrogen fertilizer on plant productivity and nitrous oxide (N2O) emissions of two pastures

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Abstract: Aims: As a consequence of global climate change, increases in the frequencies and severities of drought are anticipated for many parts of the world. Soil moisture and nitrogen (N) are among the major factors limiting grassland productivity. In pastures, N fertilizer returns by grazing animals are spatially and temporally heterogenous, and we therefore hypothesized that responses of plants and soil processes to drought may differ at the patch level. Methods: Using rain-exclusion roofs, we simulated severe summer drought in a three-year field experiment replicated at two grassland sites contrasting in climate and management intensity. The study included a factorial N application treatment encompassing the application of cattle urine and mineral nitrogen. Responses of plants, soil microbes, and soil organic matter were assessed (carbon and nitrogen pools). N2O emissions were measured on 72 dates, and soil N2O concentration profiles on 44 dates. Results: Plant productivity responded negatively to drought and positively to N application. Interestingly, no or only small drought-effect were found on plant productivity when cumulated over the entire experimental duration, despite large effects during and shortly after the period when rain-exclusion roofs were installed. We further did not find evidence for compensatory growth after drought, and drought-effects did not differ between fertilizer hot spots and unaffected areas. In the short-term, soil microbial biomass responded positively to drought, but no long-term effects were detected. Nitrous oxide (N2O) emissions originated primarily from fertilizer hot spots, and these emissions were massively reduced under drought, with effects lasting throughout most of the growing season. On a growing season basis, N2O emissions were estimated to be 1 to 2 orders of magnitude lower under drought. Conclusions: Overall, our data suggest that even severe summer drought may have relatively little effect on plant productivity in the type of grassland and climate investigated, at least when considered on an annual basis. In contrast, drought may result in a large and sustained reduction of N2O emissions.

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REGULAR ARTICLE

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may result in a large and sustained reduction of N_2O emissions.

Keywords Compensatory growth · Denitrification · Drought · Grassland · Grazing · Greenhouse gases · Soil microbial C and N · Soil acidity · Nitrification · Summer drought

Introduction

Climatic changes are anticipated as a consequence of human activities (IPCC 2007), with increased global mean temperatures being one of the most prominent effects. Global warming is expected to alter global and regional hydrological cycles, resulting in an increased frequency of climate extremes, with more frequent droughts occurring in the mid latitudes (Easterling et al. 2000; Schär et al. 2004).

Temperature, light, and precipitation impose climatic constraints on the productivity of terrestrial ecosystems, with water availability globally being the most important of these factors (Nemani et al. 2003). A very general global trend is that high productivity tends to coincide with high precipitation (e.g. Rosenzweig 1968). Less is known on effects of short-term variability in precipitation. Many field experiments have manipulated precipitation to experimentally test effects of drought. However, their results remain controversial, with some studies reporting reductions in plant productivity on an annual basis while others did not show such an effect. For example, Fay et al. (2003) reported decreased aboveground primary productivity, increased carbon allocation to roots, and decreased leaf area in tallgrass prairie exposed to drought. Similarly, Morecroft et al. (2004) reported decreased aboveground biomass accompanied by a shift in vegetation to deep-rooted and short-lived species. In contrast, Jentsch et al. (2011) found no effects on primary production in grassland ecosystems subject to repeated severe summer drought, and argued that the absence of effects was caused by complementary responses of the component species, resulting in a net buffering of the drought-effect. These studies illustrate that the responses of ecosystems to episodic drought is difficult to predict.

The productivity of natural and managed ecosystems is often also limited by the amount of nitrogen available to plants (Vitousek and Howarth 1991). An interesting question is whether effects of drought depend on nitrogen availability, i.e. whether ample supply with N can alleviate effects of drought. Such an interaction appears possible since the cycling of water and nitrogen interact through many mechanisms. For example, drought can alter the belowground allocation of plant photosynthates, thereby altering soil exoenzyme activities (Sanaullah et al. 2011) and nutrient cycling rates (Jentsch et al. 2011). Low soil moisture can also affect soil microbial processes directly by altering soil water potential, diffusion rates of gases and solutes, and redox conditions. Drought can also change plant community composition and affect N cycling processes in this way (e.g. Morecroft et al. 2004). Several studies suggest that drought responses could depend on mineral nutrition. For example, Grime and Curtis (1976) reported that high nitrogen supply protected seedlings against effects of drought. Haddad et al. (2002) found that enhanced nutrient supply promoted the stability of primary production by alleviating nutrient limitations resulting from the lock-up of nutrients in litter accumulating under drought.

Effects of drought on soil nitrogen cycling processes potentially affect emissions of nitrous oxide (N_2O) from soils. These mechanisms are important not only because N_2O constitutes a loss of nitrogen from the ecosystem, but also because N_2O is one of the most important anthropogenic greenhouse gases (IPCC 2007) and the single most important ozone depleting compound emitted today (Ravishankara et al. 2009). N_2O originates from soils as product or by-product of nitrification and denitrification (Conrad 1996; Firestone and Davidson 1989).

Pastures and rangelands are characterized by a large spatial and temporal heterogeneity in nutrient availability. Grazing animals convert plant organic nitrogen into relatively easily available forms, and re-distribute it in patchy form (Haynes and Williams 1993). Stocking densities and roaming behavior determine the total area affected by these patches, but generally only a relatively small fraction of the pasture area is affected each

year (e.g. Auerswald et al. 2010; White et al. 2001). Under cattle and sheep urine patches, local deposition rates often exceed several hundred kg N ha^{-1}. Plant growth is generally promoted by the extra nutrients available in urine patches. Urea, the main nitrogenous compound in urine, is rapidly hydrolyzed, releasing NH_4^+. High NH_4^+ concentrations stimulate nitrification and in turn denitrification, thus leading to high N_2O emissions. N_2O emissions therefore generally increase with grazing intensity (e.g. Patra et al. 2005) and are heavily dominated by urine "hot spots".

A conclusion emerging from the dramatic heterogeneity in pasture is that developing a process-based understanding of responses to drought requires studies including the patch-level (Groffman et al. 2009). Here, we present a field study in which we simulated severe summer drought in two pastures contrasting in climate and management intensity. Studying the interaction of drought with natural excreta patches is difficult for many reasons, including non-standardized patch sizes, variable N deposition rates, and the non-random location of patches. Instead, we included a factorial nitrogen fertilization treatment, encompassing the application of large amounts of cattle urine. For reference, we also included a mineral N fertilizer application. The aim of this multi-year study was to test for effects of drought on plant biomass production and nitrogen cycling, with a special emphasis on N_2O emissions. In particular, we were interested whether plant responses to drought differed under cattle urine application, and whether and how drought modified N_2O emissions from such hot spots.

Materials and methods

Field site and experimental design

In September 2006, a field experiment simulating summer drought and N deposition by grazing animals was set up. The experimental design was replicated at two research farms representing typical Swiss grassland farming systems. Both experimental sites were in flat areas (i.e. horizontal; c.f. photographs in Hartmann et al. 2011, Figs. 5 and 6 of online resource 1).

The first site, further referred to as Früebüel, is located on a montane plateau in central Switzerland east of lake Zug (47.1135°N, 8.5415°E, 1000 m a.s.l.). The growing period starts in early April and ends in late October. Before the start of the experiment, the site was managed at intermediate intensity and predominately grazed by non-dairy cattle or mown for hay three to four times per year. Vegetation was dominated by *Alopecurus pratensis*, *Dactylis glomerata*, *Trifolium repens*, and *Ranunculus bulbosus*. Other species accounting for at least a few percent cover were (in order of decreasing importance) *Lolium perenne*, *Poa pratensis*, *Poa trivialis*, *Taraxacum officinale*, *Heracleum sphondylium*, *Rumex acetosa* and *Veronica filiformis*. Prior to our experiment, the only fertilizer inputs to the site were excreta of grazing animals and the application of manure from cattle kept in the stables. Since most of this N originated from plant N from the site, net fertilizer inputs are difficult to quantify. The soil is a silt loam (37% sand, 56% silt and 7% clay) with a pH of ~4.7.

The second site, Alp Weissenstein, is an extensively managed subalpine grassland situated in a dry valley in the eastern Swiss Alps (46.5833°N, 9.7859°E, 1975 m a.s.l.). Due to the short growing period at this site (mid-May to mid-September), Alp Weissenstein is only grazed during the summer half-year. The most abundant species found at the experimental site were *Alchemilla xanthochlora* and *Festuca rubra*. *Trifolium pratense*, *Trifolium repens*, *Plantago alpina*, *Crocus albiflorus*, *Potentilla aurea*, *Leontodon hispidus*, *Crepis aurea*, *Agrostis capillaris*, *Nardus stricta*, *Phleum rhaeticum* and *Poa alpina* also exceeded a cover of several percent. Prior to our experiment, the pasture was grazed two to three times per year by non-dairy cattle and horse and no fertilizer was applied. The soil at this site is a silt loam (35% sand, 59% silt and 6% clay) with a pH of ~5.0.

In October 2006, both sites were fenced to exclude grazing animals and the experimental plots were established. These were organized in a randomized complete split-plot design with five replicate blocks per site. Each block consisted of two 3.5 × 3 m plots, of which one was subject to simulated summer drought using a rain exclusion

roof (covered with 200 μm thin plastic foil, for details see Hartmann et al. 2011). In 2007, the rain-exclusion roofs were installed from August 3 to September 27 and from July 31 to September 25 at Früebüel and Alp Weissenstein, respectively. In 2008, roofs were installed from June 26 to August 13 and from July 14 to September 26, respectively.

In each plot, a core area of 2 × 2.2 m was subdivided into four subplots by polyvinyl chloride sheets reaching to a depth of 15 cm. The subplots were either treated with ammonium nitrate (NH_4NO_3), non-dairy cattle urine, or served as unfertilized control plots (NIL). The fourth subplot remained unused. All N applications took place during periods when rain exclusion roofs were installed. Both NH_4NO_3 and urine were applied as aqueous solution (4.9 L m^{-2}) and the equivalent amount of water was applied to unfertilized control subplots (NIL treatment). Cattle urine was collected from non-dairy cattle. N fertilizers were applied as a small (5 g urine-N and 10 g NH_4NO_3-N m^{-2}) followed by a large (15 g urine-N and 30 g NH_4NO_3-N m^{-2}) application in 2007, and a single large application (15 g urine-N and 30 g NH_4NO_3-N m^{-2}) in 2008. The differences in N application rates were due to the fact that the N content of urine was known only after it had been applied to field plots. The overwhelming part of urine N is in the form of urea, which quickly hydrolyzes to ammonium in soils (Haynes and Williams 1992). As a consequence, approximately equivalent amount of NH_4^+ (after hydrolysis) were applied to the two treatments. However, our focus was not on comparing mineral fertilizer and cattle urine-treated plots, but to compare the effect of both fertilizers to the unfertilized controls individually.

Soil temperature and moisture probes were installed in two blocks per site at depths of 8 and 25 cm at Früebüel and, because of shallower soils, at 8 and 20 cm at Alp Weissenstein. The temperature probes (AD592, Analog Devices, Norwood, MA, USA) were installed in all subplots, whereas soil moisture probes (EC-6, Decagon Devices Inc., Pullman, WA, USA) were installed in unfertilized subplots only. Data were recorded as 10-min averages by an automatic data logger (CR1000, Campbell Scientific Inc., Logan, UT, USA). Precipitation at the two farms (outside the experimental site but within a few hundred meters) was measured by rain gauges (Zeeman et al. 2010). Concomitantly with the regular N_2O flux measurements described below, soil moisture was also measured in all plots using a portable soil moisture probe (ThetaProbe ML2x, Delta-T Devices Ltd., Burwell, Cambridge, UK).

During the experiment, both sites were clipped at 4 cm height. Plots at Früebüel were cut three to four times per year, concomittantly with the grazing or mowing of the surrounding pastures by the local farmer. Plots at the less productive site Alp Weissenstein were clipped only twice, once in Summer and again in Fall. A detailed chronology of the management and all field measurements is given in Supplementary Table 1.

Plant C and N

Clipped plant biomass was dried for 48 h at 65°C and weighed. The clippings were pooled per year and subplot, ground, and analyzed for carbon (C) and nitrogen (N) contents (EURO EA, HEKA tech GmbH, Wegberg, Germany). When the experiments were destructively harvested in summer 2009, roots were recovered from the top 15 cm of soils by wet sieving of ca. 600 g soil on a 0.5 mm sieve and biomass and C and N content determined.

Soil microbial C and N

Four times throughout the experiment, top soil (0–5 cm) samples were collected from all plots using a 2 cm diameter corer. Samplings took place before installation of rain exclusion roofs (2008, 2009 [the sampling would have been before the setup of the rain shelters if the experiment had been continued]) and after their removal (2007, 2008).

Soil microbial biomass C and N were measured by chloroform fumigation-extraction (Brookes et al. 1985). One sieved subsamples corresponding to 10 g dry weight was extracted with 50 mL 0.5 M K_2SO_4 (table shaker, 30 min, 200 rpm), while a second subsample was extracted after

fumigation with chloroform for 24 h. All extracts were centrifuged, filtered and organic C and N content determined using a TOC/TN-analyzer (Dimatoc-100, Dimatec, Essen, Germany). Microbial biomass C was calculated as $(C_{fumigated}-C_{unfumigated})/k_{EC}$, where $C_{fumigated}$ and $C_{unfumigated}$ are the organic C contents of fumigated and unfumigated extracts and $k_{EC} = 0.45$ is the extraction efficiency from microbial C. Microbial N was calculated similarly, using an extraction efficiency of $k_{EN} = 0.54$.

N_2O flux measurements

In November 2006, static chambers (32 cm diameter × 30 cm height) were installed in the center of all subplots. After carefully pre-trenching the soil with a spade fitting the curvature of the chamber collars, these were lowered 19 cm into the ground, resulting in 11 cm chamber height and a corresponding headspace volume of 8.85 L. To measure N_2O exchange rates, the collars were closed using a detachable lid. The static chambers were pressure-equilibrated through a 10 cm tubing section (i.d. ~3 mm) fitted with a valve. Headspace samples were collected 5, 20 and 35 min after chamber closure. Gas samples were injected into pre-evacuated exetainers and transfered to the laboratory. A gas chromatograph (Agilent 6890, Agilent Technologies Inc., Santa Clara, CA, USA) equipped with an electron capture detector was used to analyze the collected air samples for N_2O concentrations. The setup of gas chromatograph and autosampler was similar to the system described by Hedley et al. (2006), using automated injection through a 6-port valve fitted with a 250 µL loop. Ar:CH_4 (90%:10%) was used as carrier gas (20mL/min flow rate, 12′ Porapak Q 80/100 column, 80°C, isothermic). N_2O concentrations were calculated by calibration against four standard gas mixtures measured every 12 samples, using a non-linear relationship empirically derived. The long-term coefficient of variation in the concentration range up to 800 nmol mol^{-1} was ~2%, with better short-term repeatability since the long-term measurement error was mainly determined by a very slow drift of the detector. The three sequential headspace samples constituting each flux measurement were measured in succession (to minimize effects of detector drift), and N_2O flux rates calculated by linear regression of gas concentrations against time. For N_2O fluxes, the regression coefficients were generally high ($r^2 > 0.95$) unless N_2O exchange rates were close to zero. N_2O flux rates were measured 41 times at Früebüel and 31 times at Alp Weissenstein (cf. Fig. 1 and Supplementary Table 1). N_2O fluxes were measured more frequently after the application of the fertilizers.

We further measured N_2O concentrations in soil air on 21 and 23 different dates at Früebüel and Alp Weissenstein, respectively (Supplementary Table 1). Soil gas samples were collected from 50 cm polypropylene tubes (8.5 mm outer diameter, Accurel PP V8/2 HF, Membrana GmbH, Wuppertal, Germany) installed horizontally at the same depths as the soil moisture and temperature probes. These gas-permeable polypropylene tubes were closed at the ends in order to equilibrate with the soil atmosphere. On sampling dates, equilibrated air was collected with a syringe connected through a gas-tight valve, and N_2O concentrations analyzed as described above.

Soil analysis by layer

After termination of the field experiment in summer 2009, soil blocks with 20 × 20 cm surface area were excavated and divided into layers ranging from 0 to 5, 5 to 10 and 10 to 15 cm depth. In order to estimate N_2O emission and basal respiration under standardized conditions, field-moist soil samples corresponding to 100 g dry weight were sieved (4 mm mesh size) and water content adjusted to 0.3 g H_2O (g soil)$^{-1}$. The soil was then placed into 0.9 L gas-tight jars fitted with a septum and left to equilibrate at 20°C overnight. The next day, the jars were opened for 30 min to aerate the samples, closed again, and N_2O emission rates and basal respiration rates determined by measuring headspace N_2O and CO_2 concentrations after 10, 160 and 310 min.

Additional soil subsamples were sieved (4 mm mesh-size) and soil pH determined. Soil organic C and N content of these layers was determined by

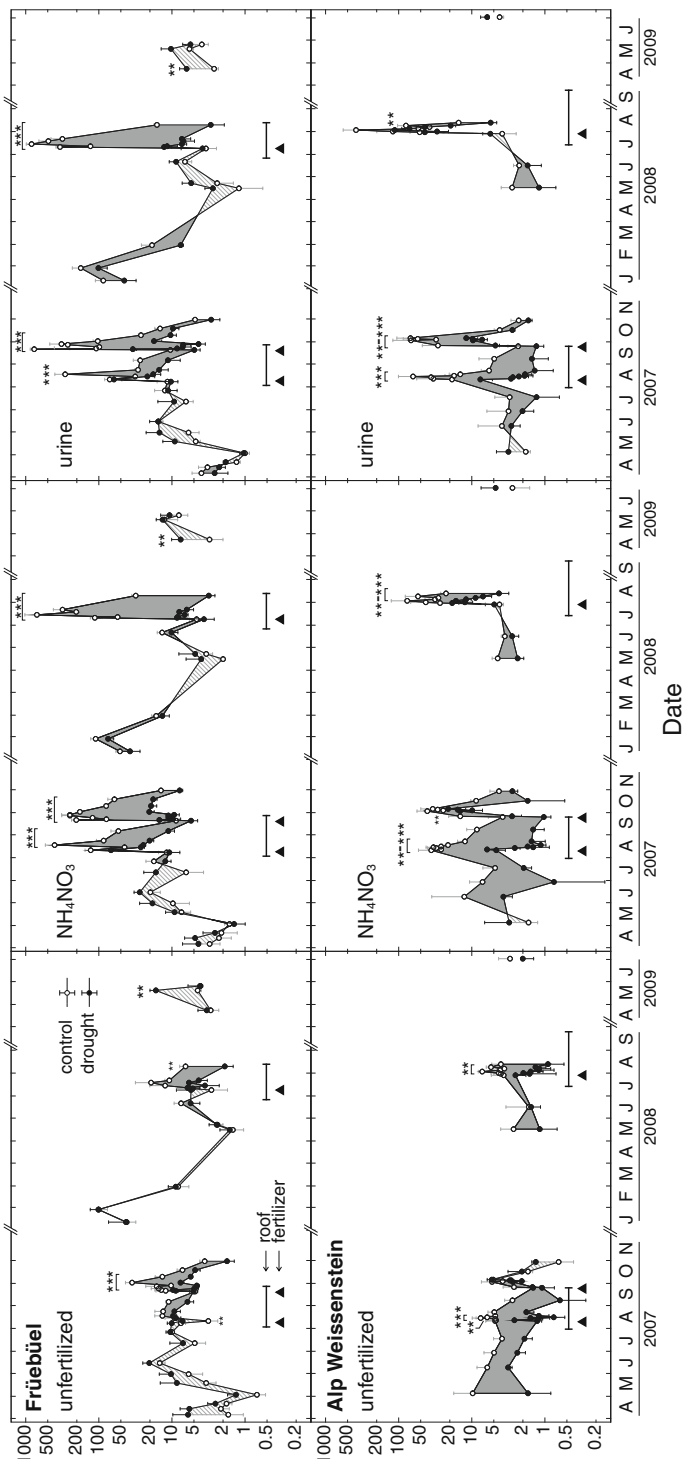

Fig. 1 Soil N_2O emission at the two experimental sites Früebüel and Alp Weissenstein. The difference between control and drought-treated plots is filled in *solid grey* when positive (i.e. N_2O emissions are reduced under drought), and hatched when negative. Note the logarithmic scale of the N_2O fluxes (Supplementary Fig. 1 shows the same data with linear scaling). *Error bars* indicate the standard errors of treatment means, and are symmetric on the log-scale but only shown in one direction for clarity. ** $P < 0.01$; *** $P < 0.001$; significance levels with $P > 0.01$ are not shown due to the large number of tests and associated increased overall type I error probability

dry combustion of sieved, root-free soil samples in an automated elemental analyzer.

Data analysis

Data were analyzed using mixed-effects models fitted by maximum likelihood (lme function from the nlme-package of R 2.12.0; R Development Core Team 2010). The models included the nested random effects site, block, plot, subplot, and, where appropriate, soil layer. Drought, fertilization, and, where appropriate, soil depth, were the fixed effects tested. Biomass and flux data were log-transformed in order to test for differences in relative effects of treatments (treatment interaction terms); this also led to a homoscedastic residual distribution. Time series were analyzed using the same models but including time as continuous or ordered factor. An appropriate temporal covariance structure between repeated measurements on the same subject was selected (e.g. uniform correlation or autoregressive model of 1st order). In general, the correlation between repeated measurements was very weak and the choice of correlation structure therefore did not matter. Differences were considered significant when $P < 0.05$. All error estimates in text and figures are standard errors of treatment means.

Results

Soil temperature and moisture

Soil temperature was not affected by the experimental treatments (Table 1). Soil moisture exhibited large intra-annual variation with pronounced natural drying cycles. The rain exclusion roofs reduced precipitation in drought-treated plots in Früebüel by 450 and 410 mm in 2007 and 2008, respectively. The corresponding reductions in precipitation at the dryer site Alp Weissenstein were 210 and 315 mm in 2007 and 2008, respectively. This corresponds to reductions of 25–30% on an annual and of 30–40% on a growing season basis at both sites.

Soil moisture was reduced by 40–60% in the period where the rain exclusion roofs were installed ($P < 0.001$ for both sites). The soil moisture reductions persisted for several weeks or even months after removal of the rain exclusion roofs, an effect discussed in detail in Hartmann et al. (2011).

Plant biomass and nitrogen

Plant productivity responded negatively to drought and positively to N application. However, these responses were mostly restricted to the period during which the rain exclusion roofs were installed, and the weeks immediately after fertilizer application ($P < 0.001$ for time × N and time × drought). Expressed as cumulated productivity over the experimental duration, treatment effects were much smaller (−9% for drought, $P < 0.01$) or absent (N fertilizer, c.f. Supplementary Table 3).

The clipping of plots was timed based on agricultural practice and thus not synchronized with the setup of the rain exclusion roofs. We therefore analyzed biomass production from the last clipping before roof setup until the first clipping after removal of the roofs. During this period, aboveground biomass production dropped by 35% ($P < 0.001$) under drought, an effect which was more pronounced at Alp Weissenstein (site × drought, $P < 0.05$). Both N fertilizers increased aboveground biomass production (∼+40%, $P < 0.001$). Belowground biomass harvested at the end of the experiment (2009) was affected by neither treatmet.

Plant N removed with the clippings dropped under drought (Table 3, −19%, $P < 0.01$) and increased with fertilization (+30%, $P < 0.001$). Interestingly, these effects did not persist into 2009, the year when the experiment was terminated (no rain exclusion roofs were set up in 2009 and no fertilizer applied). Root biomass N remained unaffected by drought and urine application, but increased with NH_4NO_3 application ($P < 0.05$).

Soil and microbial carbon and nitrogen

Neither drought nor fertilization affected soil C and N pools (Tables 2 and 3). Soil microbial biomass averaged 1.10 ± 0.02 mg C (g soil)$^{-1}$ at Früebüel and 2.15 ± 0.05 mg C (g soil)$^{-1}$

Table 1 Precipitation, soil temperature and soil moisture of control and drought treated soils at the two study sites Früebüel and Alp Weissenstein

Site and month	Precipitation (mm)			Soil temperature (°C)			Soil moisture (m^3 H_2O m^{-3})					
	2007	2008	2009	2007	2008	2009	2007		2008		2009	
							Control	Drought	Control	Drought	Control	Drought
Früebüel												
January	102	52	33	3.4	1.9	1.4	0.37	0.37	0.41	0.35	0.39	0.37
February	55	43	110	2.8	1.8	1.6	0.37	0.37	0.39	0.34	0.41	0.40
March	149	104	115	3.6	3.2	1.4	0.38	0.38	0.42	0.36	0.43	0.40
April	13	202	56	9.6	5.7	7.1	0.33	0.33	0.43	0.38	0.39	0.38
May	209	46	184	11.8	12.1	11.6	0.34	0.34	0.29	0.26	0.41	0.41
June	238	196	294	15.9	16.0		0.35	0.35	0.33	0.30		
July	317	290	120	17.2	17.8		0.41	0.40	0.37	0.18		
August	336	293	16.9	17.2			0.42	0.35	0.39	0.13		
September	131	187	14.5	13.1			0.41	0.24	0.39	0.29		
October	64	152	10.9	10.6			0.40	0.25	0.40	0.34		
November	37	46		5.1	5.1		0.41	0.33	0.42	0.38		
December	114	44		2.9	2.8		0.42	0.36	0.41	0.38		
Sum/Mean	1,765	1,656		9.5	8.9		0.38	0.34	0.39	0.31		
Alp Weissenstein												
January	82[a]	66[a]	46[a]		0.9	1.4			0.47	0.42	0.49	0.50
February	48[a]	11[a]	81[a]		0.8	1.6[b]			0.47	0.43	0.50[c]	0.50[c]
March	54[a]	52[a]	44[a]		0.9	1.7[b]			0.51	0.46	0.50[c]	0.50[c]
April	18	84	87		3.0[b]	3.3[b]			0.50	0.50	0.50[c]	0.50[c]
May	112	101	43		8.2	9.3			0.50	0.48	0.47	0.44
June	166	140	120	17.2	11.0	10.0	0.56	0.55	0.48	0.47	0.42	0.44
July	123	217	61	14.2	12.6	11.9[b]	0.50[c]	0.50[c]	0.47	0.49	0.39	0.34
August	172	117		13.6	13.6		0.55	0.19	0.50	0.33		
September	48	148		9.6	10.1		0.48	0.31	0.50	0.10[d]		
October	19	75		6.5	7.0[b]		0.48	0.43	0.40[c]	0.10[d]		
November	105[a]	107[a]		2.4[b]	2.4		0.50[c]	0.50[c]	0.53	0.50		
December	25[a]	73[a]		0.2[b]	1.7		0.50[c]	0.50[c]	0.52	0.51		
Sum/Mean	970	1,189			6.2				0.49	0.40		

The N fertilization treatment did not affect these parameters. Summer precipitation was measured by rain-gauges installed at the two farms (for details, see Zeeman et al. 2010)

[a]Data interpolated based on measurements from a nearby weather station with heated rain-gauge

[b]Data interpolated based on soil temperature readings at the next weather station

[c]Visually estimated interpolated due to incomplete logger data

[d]Very dry soils; soil moisture readings outside calibrated range

at Alp Weissenstein. Variable treatment effects were found over the duration of the experiment (Supplementary Tables 2 and 3). An important general trend was for increased microbial C or C:N, respectively, after drought exposure. In 2007, microbial C increased by 11% ($P < 0.05$, average of both sites) and C:N increased by 17% at Alp Weissenstein but not at Früebüel ($P < 0.001$ for drought and $P < 0.01$ for drought × site). In 2008, microbial C increased by 41% under drought at Alp Weissenstein but not at Früebüel ($P < 0.01$ for drought and $P < 0.05$ for drought × site). C:N increased by 26% (average of both sites, $P < 0.001$). No drought effects were found before setup-of the roofs in 2008 and at the end of the study in 2009. Another general trend was for decreased microbial C and N under NH_4NO_3 but not under urine application This effect manifested on several dates and was mainly driven by a decrease in microbial C and N at Früebüel (13% decreased for C and N at Früebüel, average over all measurements).

Table 2 C pools (g C m^{-2}) in plants and soil organic matter

Site	Date	C content (g m^{-2})						Significance[a]		
		Control			Drought					
Fraction		NIL	NH_4NO_3	Urine	NIL	NH_4NO_3	Urine	D	N	D × N
Früebüel										
Plants										
Clipping	16-MAY-2007	~150–170, pre-treatment clipping, not separated by plots						n.a.	n.a.	n.a.
Clipping	11-JUL-2007	161 ± 11	173 ± 7	174 ± 13	182 ± 17	176 ± 13	171 ± 12	n.s.	n.s.	n.s.
Clipping	17-SEP-2007	35 ± 3	58 ± 3	44 ± 3	29 ± 2	31 ± 2	32 ± 3	**	***	*
Clipping	22-NOV-2007	68 ± 11	77 ± 9	80 ± 9	44 ± 7	57 ± 6	55 ± 6	*	n.s.	n.s.
Clipping	10-JUN-2008	157 ± 12	128 ± 9	123 ± 5	148 ± 16	131 ± 11	122 ± 16	n.s.	*	n.s.
Clipping	07-JUL-2008	84 ± 6	84 ± 5	87 ± 10	108 ± 20	91 ± 4	90 ± 5	n.s.	n.s.	n.s.
Clipping	30-SEP-2008	109 ± 7	148 ± 21	111 ± 19	72 ± 11	101 ± 19	109 ± 22	*	*	*
Shoots	26-MAY-2009	190 ± 17	208 ± 41	199 ± 22	218 ± 24	167 ± 30	232 ± 29	n.s.	n.s.	n.s.
Roots[b]	26-MAY-2009	1045 ± 80	939 ± 52	978 ± 160	1188 ± 169	1436 ± 271	818 ± 75	n.s.	n.s.	n.s.
Cumulated clippings	2007–2009 Shoots only	965 ± 39[c]	1037 ± 71[c]	977 ± 49[c]	961 ± 73[c]	913 ± 37[c]	971 ± 78[c]	n.s.	n.s.	n.s.
Soil										
SOM[bd]	26-MAY-2009	5177 ± 678	5252 ± 774	5629 ± 726	5744 ± 655	5397 ± 808	5888 ± 747	n.s.	n.s.	n.s.
Alp Weissenstein										
Plants										
Clipping	03-JUL-2007	153 ± 6	139 ± 14	132 ± 23	121 ± 9	97 ± 16	132 ± 10	n.s.	n.s.	*
Clipping	21-SEP-2007	72 ± 7	109 ± 8	101 ± 5	28 ± 2	39 ± 9	46 ± 4	**	**	n.s.
Clipping	14-JUL-2008	151 ± 19	197 ± 34	178 ± 19	165 ± 11	199 ± 22	198 ± 7	n.s.	n.s.	n.s.
Clipping	04-OCT-2008	68 ± 8	105 ± 8	131 ± 8	47 ± 11	63 ± 10	95 ± 9	**	***	n.s.
Shoots	13-JUL-2009	146 ± 9	137 ± 11	139 ± 7	131 ± 9	127 ± 6	145 ± 5	n.s.	n.s.	n.s.
Roots[b]	13-JUL-2009	1471 ± 146	1509 ± 79	1451 ± 83	1506 ± 112	1620 ± 237	1484 ± 139	n.s.	n.s.	n.s.
Cumulated clippings	2007–2009 Shoots only	590 ± 16	686 ± 42	680 ± 42	492 ± 24	525 ± 55	616 ± 10	*	*	n.s.
Soil										
SOM[bd]	13-JUL-2009	9248 ± 1883	9239 ± 1970	8222 ± 1806	8809 ± 1789	9337 ± 2066	10216 ± 2355	n.s.	n.s.	n.s.

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

[a]Drought is abbreviated as D

[b]Roots and soil organic matter refer to the top 15 cm of the soil profile

[c]Including an estimated 160 g C m^{-2} from the pre-treatment clipping

[d]Soil organic C content was only analysed in 2 out of 5 blocks per site

N_2O emissions

N_2O emissions from unfertilized subplots (NIL) were higher at the more intensively managed site Früebüel than at Alp Weissenstein (Fig. 1). At both sites, the N fertilizers strongly increased N_2O emissions, with a marked peak during the first days after N application. N_2O emissions thereafter decreased by several orders of magnitude, but often were still increased at the end of the season when snow cover prevented further measurements.

N_2O fluxes were very dynamic over time and could not be predicted based on simple indicators (e.g. soil moisture). We roughly estimated effects on the seasonal balance by assuming that our samples were representative of the N_2O flux distribution over the growing season. Considering that N_2O fluxes followed a log-normal distribution (i.e. were normally distributed on a *log*-scale), the average seasonal N_2O flux can be estimated as $exp(\mu_{log} + \sigma^2_{log}/2)$, where μ_{log} and σ_{log} are the mean and standard deviation of the logarithm of the measured fluxes. This was done separately for the period before and after fertilizer application, because the N fertilizers substantially increased N_2O fluxes relative to the pre-application period. Fluxes of both periods then were added. Average growing-season N_2O emissions (Fig. 2) were increased by the N fertilizers at both sites ($P < 0.001$), with a tendency for a larger stimulation of N_2O emissions under urine application, at least when plots were exposed to natural precipitation. In 2007, simulated drought strongly reduced the N

Table 3 N pools (g N m^{-2}) in plants and soil organic matter (SOM)

Site	N content (g m^{-2})						Significance[a]		
	Control			Drought					
Fraction	NIL	NH_4NO_3	Urine	NIL	NH_4NO_3	Urine	D	N	D × N
Früebüel									
Plant N									
Cumulated clippings[b]	28.1 ± 2.4	38.9 ± 1.9	30.5 ± 1.9	26.7 ± 2.6	31.4 ± 1.6	29.0 ± 2.2	n.s.	**	n.s
Final harvest									
Shoots	7.81 ± 0.68	10.93 ± 2.75	7.42 ± 0.81	9.94 ± 1.18	9.13 ± 0.79	10.24 ± 1.53	n.s.	n.s.	n.s.
Roots	36.0 ± 7.3	34.4 ± 7.0	29.4 ± 4.3	35.6 ± 7.2	44.4 ± 9.1	27.1 ± 3.4	n.s.	n.s.	n.s.
Soil N									
SOM	450 ± 66	431 ± 153	495 ± 48	561 ± 19	538 ± 42	569 ± 43	n.s.	n.s.	n.s.
Alp Weissenstein									
Plant N									
Cumulated clippings	19.7 ± 1.0	30.5 ± 2.5	27.9 ± 1.8	15.2 ± 2.0	20.0 ± 2.3	21.2 ± 0.8	**	***	n.s.
Final harvest									
Shoots	6.97 ± 0.63	6.75 ± 0.35	7.17 ± 0.87	7.97 ± 0.74	7.22 ± 0.33	7.18 ± 0.53	n.s.	n.s.	n.s.
Roots	42.4 ± 7.5	60.1 ± 8.2	43.7 ± 3.6	53.8 ± 6.9	72.7 ± 10.1	59.6 ± 9.8	n.s.	*	n.s.
Soil N									
SOM	808 ± 22	792 ± 14	702 ± 91	707 ± 39	818 ± 112	909 ± 223	n.s.	n.s.	n.s.

Root N and soil organic matter N refer to the 0–15 cm horizon. Soil organic matter N was estimated only in 2 out of 5 blocks
$*P < 0.05$; $**P < 0.01$; $***P < 0.001$
[a]Drought is abbreviated as D
[b]Excluding the initial pre-treatment cut

fertilization-effect (by a factor of 3 and 15 at Alp Weissenstein and Früebüel, respectively, N-effect expressed as stimulation relative to emissions in the NIL plots; $P = 0.013$ for site × drought × N, $P = 0.003$ for site × N, $P < 0.001$ for drought × N). In 2008, the temporal coverage of N_2O emission measurements was too low to estimate a seasonal balance at Alp Weissenstein. At Früebüel, drought reduced the fertilizer effect on N_2O emissions by nearly two orders of magnitude (Fig. 2).

Soil N_2O concentrations

Growing-period soil N_2O concentrations in unfertilized soils increased with depth (8 cm: 394 ± 25

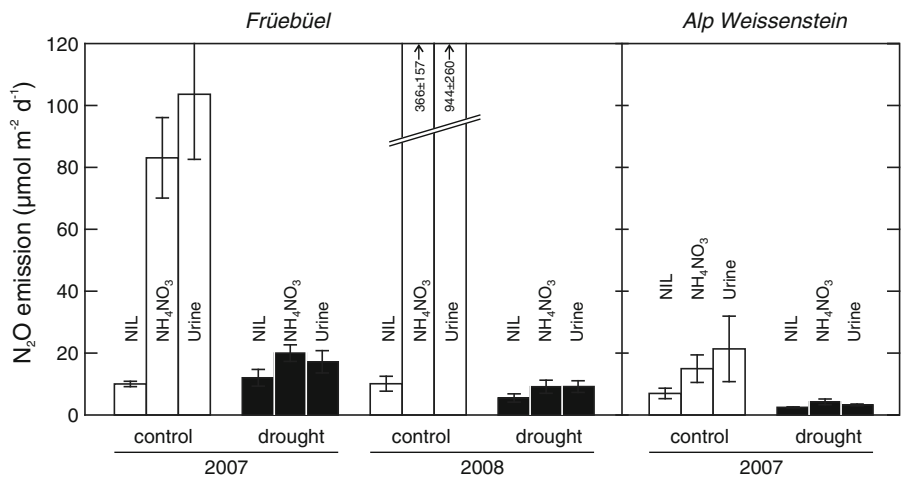

Fig. 2 Estimated mean N_2O emission at the two experimental sites Früebüel and Alp Weissenstein (April 1 until October 31). No balance was calculated for Alp Weissenstein in 2008 due to poor season coverage. *Error bars* indicate the standard errors of treatment means

ppb; 20–25 cm: 494 ± 52 ppb; $P < 0.05$; average of measurements conducted on 21 [Früebüel] and 23 [Alp Weissenstein] different dates, respectively, see Supplementary Table 1). Fertilizer application increased soil N_2O concentrations, an effect which was most evident during the 14 days following N application (+220 and +280% for NH_4NO_3 and urine, respectively; $P < 0.01$). The fertilizer-effect was higher at Früebüel than at the more extensively managed site Alp Weissenstein ($P < 0.05$ for site × N). Effects of fertilizer application were substantially smaller when applied under drought than when applied under ambient soil moisture (drought × fertilization, $P < 0.05$).

During periods with installed rain shelters, soil N_2O concentrations were reduced by 60% ($P < 0.05$) compared to unsheltered soils. However, this effect was mainly driven by the much lower increase in soil N_2O concentrations when fertilizer was applied under drought, with little or no effect of drought in the absence of fertilization (−30%, n.s.).

N_2O emission and basal respiration of sieved soil layers

N_2O emission rates of sieved soils exposed to standardized soil moisture and temperature decreased with soil depth (Table 4, $P < 0.001$ for depth). At Früebüel, this effect was less pronounced than at Alp Weissenstein ($P < 0.001$ for site × depth). Drought had no effect on N_2O emissions, while fertilization with NH_4NO_3 reduced N_2O emission rates in 0–5 cm soil depth (N × depth, $P < 0.05$).

Soil basal respiration (Table 3) at both sites decreased with depth ($P < 0.001$), an effect which was less pronounced at Früebüel than at Alp Weissenstein ($P < 0.05$ for site × depth). Fertilization with NH_4NO_3 and urine reduced soil basal respiration ($P < 0.001$, −22% and −11% for NH_4NO_3 and urine, respectively). However, application of NH_4NO_3 reduced soil basal respiration in all layers, while cattle urine only had an effect in the 0–5 cm depth layer (N × depth, $P < 0.05$).

Soil pH

Soil pH (Table 3) was affected by N fertilization, and this effect depended on soil depth ($P < 0.001$

Table 4 N_2O emissions, basal respiration and soil pH of field-sampled soil incubated in the laboratory (20°C, water content adjusted to 0.3 m^3 H_2O m^{-3})

Site and	N_2O emissions (pmol (g soil)$^{-1}$ d^{-1})			Basal respiration (μmol CO_2 (g soil)$^{-1}$ d^{-1})			Soil pH		
fertilizer	0–5 cm	5–10 cm	10–15 cm	Average	0–5 cm	5–10 cm	10–15 cm	Average	0–5 cm	5–10 cm	10–15 cm	Average
Früebüel												
NIL	157 ± 33	63 ± 14	22 ± 8	84 ± 17	5.60 ± 0.37	2.68 ± 0.12	1.85 ± 0.07	3.37 ± 0.32	4.86 ± 0.08	4.66 ± 0.07	4.69 ± 0.09	4.74 ± 0.05
NH_4NO_3	116 ± 34	60 ± 15	52 ± 5	79 ± 15	4.29 ± 0.21	2.08 ± 0.10	1.78 ± 0.08	2.72 ± 0.22	4.31 ± 0.06	4.38 ± 0.06	4.55 ± 0.07	4.41 ± 0.04
Urine	279 ± 77	80 ± 21	54 ± 17	143 ± 34	5.13 ± 0.49	2.63 ± 0.14	2.08 ± 0.14	3.28 ± 0.30	4.93 ± 0.07	4.76 ± 0.06	4.87 ± 0.10	4.85 ± 0.05
Alp Weissenstein												
NIL	1133 ± 318	85 ± 21	77 ± 17	444 ± 142	15.83 ± 1.27	3.41 ± 0.14	1.95 ± 0.10	7.06 ± 1.23	5.20 ± 0.07	4.81 ± 0.07	4.69 ± 0.07	4.90 ± 0.06
NH_4NO_3	312 ± 63	101 ± 21	58 ± 15	166 ± 33	11.30 ± 0.41	2.95 ± 0.27	1.84 ± 0.17	5.36 ± 0.80	4.70 ± 0.06	4.56 ± 0.08	4.57 ± 0.08	4.61 ± 0.04
Urine	1332 ± 195	103 ± 29	50 ± 11	510 ± 131	13.02 ± 0.67	3.21 ± 0.28	1.86 ± 0.09	6.03 ± 0.95	5.08 ± 0.08	4.73 ± 0.07	4.70 ± 0.08	4.84 ± 0.05
Average	562 ± 90	84 ± 9	52 ± 6		9.19 ± 0.63	2.83 ± 0.09	1.89 ± 0.05		4.84 ± 0.05	4.65 ± 0.03	4.68 ± 0.03	

Data for the drought treatments are combined since the drought-effect was not statistically significant

for N and N × depth). A closer examination revealed that this effect was essentially driven by a decrease in top soil pH under NH_4NO_3 fertilization ($P < 0.001$ for the linear contrast comparing NH_4NO_3 to unfertilized subplots, and its interaction with soil depth). No such significant effects were detected for the urine application treatment.

Discussion

The simulation of summer drought using rain exclusion roofs reduced annual precipitation by 25–30% and resulted in substantially lower soil moisture. Interestingly, lower soil moisture prevailed for several months after removal of the rain shelters because soils re-saturated only slowly (cf. Table 1 and Hartmann et al. 2011). During the most extreme periods of the drought, plants showed symptoms of severe water stress, as evidenced in a loss of turgor pressure and withering, and growth was reduced. Interestingly, however, only a rather small reduction in plant productivity was found on an annual basis or when integrated over the entire duration of the experiment.

In response to biomass removal by clipping or grazing, compensatory growth is often observed (Oesterheld and McNaughton 1991). Many studies have demonstrated that the extent of compensatory growth can depend on the amount of resources available to plants (e.g. Hilbert et al. 1981; van Staalduinen and Anten 2005) and be plant functional type-dependent (Coughenour et al. 1990; Hawkes and Sullivan 2001; Oesterheld 1991). Compensatory growth also occurs after drought (Hall 1993; Horst and Nelson 1979). In our study, such compensatory responses were not evident. No statistically significant increases in the biomass of drought-treated plots compared to control plots were found. It has been argued that high nitrogen supply may reduce the impact of drought on plants. The mechanisms involved include, for example, the improvement of recruitment by high N supply (Grime and Curtis 1976) and compensation for N limitations on growth due to nutrients locked up in undecomposed litter (Haddad et al. 2002). In our study, drought-effects depended on N-supply (and vice versa) on some dates; however, aboveground productivity was not improved by N under drought. The beneficial effect of extra N supplied also was *lower* under drought than under control conditions, because plants were unable to use the extra resource under the water limitation imposed.

Integrated over the entire experimental duration, N-effects on productivity were absent at one site (Früebüel), and did not significantly depend on drought at either site. The small productivity response to N fertilization at one site and the absence of effects at the more productive site may indicate that this nutrient was not particularly limiting. We argue that the absence of effects is unlikely to be the result of a lack of statistical power, since effects of 10 and 15% would have been detected with a power of 50 and 80% (Montecarlo simulations based on variance component estimates from our data, significance level $\alpha = 0.05$).

In our study, N_2O emissions decreased under simulated drought, and more so when plots were fertilized. Conversely, fertilizer addition massively increased N_2O emissions, especially when soil moisture was moderate to high. These interactive effects can easily be understood in the light that N_2O production from denitrification is generally much larger than emissions from nitrification. Nitrification dominates N_2O emissions when water filled pore space is below ~60%, i.e. when soils are relatively dry (Linn and Doran 1984). At higher soil moisture, nitrification becomes limited by a lack of oxygen, but redox potential can drop low enough within microsites to enable the release of comparably large amounts of N_2O from denitrification (Beare et al. 2009; Dobbie et al. 1999; Flechard et al. 2007; Smith et al. 1998), at least when NO_3^- and oxidizable organic substrate are available in sufficient quantities (Weier et al. 1993). When the rain exclusion roofs were installed, no wetting of soils could occur. After removal of the roofs, the re-saturation of the soils to levels comparable to the ones in the unsheltered control plots took several weeks to months (cf. Hartmann et al. 2011), so that the critical threshold where denitrification kicks in was only seldom reached. Low soil moisture can also limit the activity of nitrifying micro-organisms (Linn

and Doran 1984), and it therefore appears possible that this effect led to a further reduction of N_2O emissions from plots experiencing simulated drought. Under some circumstances, dry soils can even turn into a N_2O sink (Flechard et al. 2005). Reductions of N_2O emissions under drought have been reported from studies in forest (e.g. Davidson et al. 2008; Goldberg and Gebauer 2009; van Haren et al. 2005), but to the best of our knowledge the present study is the first to report effects on N_2O emissions under simulated drought in grassland. The fertilizer additions simulating N deposition by grazing animals lead to N_2O emissions that were comparable to the ones reported in other studies (e.g. de Klein et al. 2003; Dobbie 2003). N_2O fluxes peaked during the first days after application, exceeding control levels by up to two orders of magnitude; N_2O fluxes were, however, very dynamic, and often remained elevated for several weeks, so that a precise assessment of cumulated N_2O emissions would have required very frequent, automated, measurements. Nevertheless, we are confident that growing-season emissions increased by one to two orders of magnitude at Früebüel and more than doubled at Alp Weissenstein. The striking difference between sites regarding their responses to N addition can be understood in light of the higher management intensity, the lower N limitation, and the smaller plant growth responses at Früebüel, which will likely have resulted in a higher fraction of the applied N becoming available for nitrification and denitrification.

N_2O emissions generally peaked after nitrogen addition or precipitation. Events of this type have been termed "hot moments", and are characterized by rapid changes which bring together the environmental conditions and compounds required for a certain process to take place (here: nitrate, organic carbon, and anaerobic conditions). Under drought, organic substrate and mineral nitrogen may accumulate and the rapid wetting upon the first precipitation may also release extra organic C and N due to cell lysis (cf. Fierer and Schimel 2003). Regardless of the mechanisms involved, N_2O emission bursts after re-wetting are not uncommon (e.g. Beare et al. 2009; Flessa et al. 1995; Prieme and Christensen 2001). However, in our study, no substantial increase in N_2O emissions in drought-treated relative to unsheltered control plots were detected upon the first re-wetting after roof removal.

Other "hot moments" in terrestrial ecosystems are freeze-thaw cycles as they occur in early spring. These can trigger N_2O emissions that make up for a substantial fraction of annual N_2O emissions (e.g. Flessa et al. 1995; Herrmann and Witter 2002; Prieme and Christensen 2001). In our study, the largest emissions of N_2O from unfertilized plots were indeed recorded in Spring 2008. However, our measurements were not frequent enough to estimate the total emissions due to these events; we also are unable to test whether potentially compensatory effects (e.g. due to the mineralization of organic substrate that accumulated under drought) occurred in this period. The single spring-time measurement showing such large N_2O fluxes did not show an effect of drought.

Fertilization with NH_4NO_3 did not stimulate N_2O emissions more than fertilization with urine, despite containing double the amount of N. NH_4NO_3 application also resulted in a decrease in microbial C and N, a decrease in soil basal respiration, and decreased N_2O production in our aerobic laboratory incubations. The latter incubations were conducted at low soil moisture, and soils were well-aerated as consequence of sieving; we therefore argue that the measured N_2O production is indicative of nitrification rates. These responses are likely to be due to the drop in top-soil pH observed under NH_4NO_3 application. Nitrification indeed is strongly inhibited at low soil pH (Prosser 1989), and N_2O emissions often decrease with soil acidity (grassland: Yamulki et al. 1997; forest: Sitaula et al. 1995; Weslien et al. 2009). In the sequence of soil N transformations, nitrification is upstream of denitrification, and it is therefore likely that an inhibition of nitrification would also reduce emissions originating from denitrification (which by itself may also be sensitive to pH changes). The ratio of growing season N_2O emissions from NH_4NO_3 and urine-treated plots decreased from ~1.2 in 2007 to 0.5 in 2008 (averages across sites), supporting our hypothesis of progressive top-soil pH reductions as driver of

these effects. Urine application may also have increased N_2O emissions from denitrification due to extra C released from scorched roots (e.g. Carter et al. 2006).

Interestingly, drought lead to increased microbial biomass and increased microbial C:N in the short term. Increased microbial C:N might indicate the increased importance of fungal biomass under drought. Drought may also have led to increased belowground allocation of plants and thus higher substrate availability and biomass of soil heterotrophs. These effects, however, were only observed in the short term and did not carry over into the next year.

Conclusions

Grazed ecosystems cover a substantial fraction of the global land surface (Loveland et al. 2000), with many located in areas potentially affected by future climate extremes. Effects of drought on N_2O emissions have rarely been studied in these systems, despite their significant contribution to greenhouse gas emissions from agriculture (IPCC 2007). A characteristic of grazed ecosystem is their spatial heterogeneity, giving rise to the possibility of small-scale variation in the responses of processes to drought. Also, effects observed during actual drought can potentially be compensated by various mechanisms after soil moisture reverts to normal levels.

Plant productivity was strongly reduced during the actual drought; however, despite the absence of evidence for compensatory growth following drought, productivity remained remarkably stable on an annual basis. Drought-effects also did not differ between simulated fertilizer hot spots and unaffected areas. In contrast, N_2O emissions were found to originate primarily from fertilizer hot spots, and drought led to a large reduction of N_2O emissions, particularly from these hot spots. Effects on plant growth and N_2O emissions may be linked inasmuch as the absence of plant growth responses even under largely increased nutrient input did not contribute to removing these nutrients from soil, so that these fully became available for nitrification and denitrification.

Overall, our data suggest that summer drought may have little effect on plant productivity in the type of grassland and climate investigated, but result in a large reduction of net emissions of N_2O (and also CH_4, see Hartmann et al. 2011) from these ecosystems.

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